

## VULNERABILITY TO XYLEM CAVITATION AND THE DISTRIBUTION OF SONORAN DESERT VEGETATION<sup>1</sup>

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We studied 15 riparian and upland Sonoran desert species to evaluate how the limitation of xylem pressure ( $\Psi_x$ ) by cavitation corresponded with plant distribution along a moisture gradient. Riparian species were obligate riparian trees (*Fraxinus velutina*, *Populus fremontii*, and *Salix gooddingii*), native shrubs (*Baccharis* spp.), and an exotic shrub (*Tamarix ramosissima*). Upland species were evergreen (*Juniperus monosperma*, *Larrea tridentata*), drought-deciduous (*Ambrosia dumosa*, *Encelia farinosa*, *Fouquieria splendens*, *Cercidium microphyllum*), and winter-deciduous (*Acacia* spp., *Prosopis velutina*) trees and shrubs. For each species, we measured the “vulnerability curve” of stem xylem, which shows the decrease in hydraulic conductance from cavitation as a function of  $\Psi_x$  and the  $\Psi_{crit}$  representing the pressure at complete loss of transport. We also measured minimum in situ  $\Psi_x$  ( $\Psi_{xmin}$ ) during the summer drought. Species in desert upland sites were uniformly less vulnerable to cavitation and exhibited lower  $\Psi_{xmin}$  than riparian species. Values of  $\Psi_{crit}$  were correlated with minimum  $\Psi_x$ . Safety margins ( $\Psi_{xmin} - \Psi_{crit}$ ) tended to increase with decreasing  $\Psi_{xmin}$  and were small enough that the relatively vulnerable riparian species could not have conducted water at the  $\Psi_x$  experienced in upland habitats (–4 to –10 MPa). Maintenance of positive safety margins in riparian and upland habitats was associated with minimal to no increase in stem cavitation during the summer drought. The absence of less vulnerable species from the riparian zone may have resulted in part from a weak but significant trade-off between decreasing vulnerability to cavitation and conducting efficiency. These data suggest that cavitation vulnerability limits plant distribution by defining maximum drought tolerance across habitats and influencing competitive ability of drought tolerant species in mesic habitats.

**Key words:** comparative approach; Sonoran desert vegetation; species distribution; xylem cavitation; xylem conducting efficiency; water relations.

Uninterrupted transport of water through the xylem is essential for plant growth and survival because it replaces water lost by transpiration and allows stomata to remain open for photosynthesis. Water moves through the xylem under negative pressure (Pockman, Sperry, and O’Leary, 1995; Sperry et al., 1996; Tyree, 1997), which is limited in magnitude by cavitation: the sudden change from liquid to vapor phase within normally water-filled xylem conduits. Does this physical limitation on water transport correspond with species distributions with respect to water availability? We addressed this question by surveying cavitation vulnerability of stem xylem across Sonoran desert species adapted to a wide range of water availability from riparian to desert upland habitats.

Water-stress-induced cavitation occurs when the xylem pressure ( $\Psi_x$ ) becomes sufficiently negative to overcome the capillary forces of water in the pit membrane pores connecting adjacent air- and water-filled xylem conduits (Zimmermann, 1983; Crombie, Hipkins, and Milburn, 1985; Tyree and Sperry, 1989). The  $\Psi_x$  required for cavitation is determined at least in part by the diameter of the membrane pores; smaller pores allow more negative  $\Psi_x$  before cavitation occurs (Zimmermann, 1983; Jarbeau, Ewers, and Davis, 1995). The result of cavitation is a vapor- and air-filled conduit that no longer trans-

ports water. The accumulation of such “embolized” conduits reduces xylem hydraulic conductance ( $k_x$ ).

Modeling studies have investigated the consequences of xylem cavitation for limiting the range of possible  $\Psi_x$  allowing water uptake through the soil–plant continuum (Tyree and Sperry, 1988; Sperry et al., 1998). For most plants and soils the minimum  $\Psi_x$  allowing water uptake and transport ( $\Psi_{crit}$ ) corresponds to the  $\Psi_x$  causing complete loss of  $k_x$ . Exceptions may occur when hydraulic failure occurs in the soil rather than the xylem owing to coarse soil texture or limited surface area of absorbing roots. In these cases, the  $\Psi_{crit}$  is less negative than what would eliminate xylem transport (Sperry et al., 1998). Thus, the  $\Psi_x$  causing failure of xylem transport represents a conservative (i.e., most negative) estimate for  $\Psi_{crit}$ . Unless noted, we will use this definition of  $\Psi_{crit}$  throughout this paper. If the actual  $\Psi_x$  in a plant were ever to drop to  $\Psi_{crit}$ , all water transport would be eliminated and the plant must either cease gas exchange or suffer the effects of rapid and severe dehydration of its foliage.

Available evidence suggests that the  $\Psi_{crit}$  limit is of biological and ecological significance, because it appears to correspond with the physiological range of  $\Psi_x$  in plants. In many mesic species, minimum  $\Psi_x$  approaches within a few tenths of a megapascal of  $\Psi_{crit}$  on a daily basis, suggesting that stomata regulate transpiration to avoid driving  $\Psi_x$  below  $\Psi_{crit}$  (Tyree and Sperry, 1988; Sperry, Alder, and Eastlack, 1993; Sperry and Pockman, 1993; Hacke and Sauter, 1995; Salendra, Sperry, and Comstock, 1995; Alder, Sperry, and Pockman, 1996). Furthermore, a review of 37 species from mesic and xeric habitats showed that  $\Psi_{crit}$  and in situ  $\Psi_x$  were correlated (Sperry, 1995). The  $\Psi_{crit}$  of most mesic plants was not sufficiently negative to allow water transport under the low  $\Psi_x$  observed for xeric plants.

Why might safety margins above  $\Psi_{crit}$  tend to be small? One

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TABLE 1. Species names, abbreviations, family, habitat (R, riparian; F, floodplain; U, upland) and habit (DD, drought deciduous; WD, winter deciduous; PS, photosynthetic stems; E, evergreen) of the species used for comparative study of vulnerability to cavitation in the Sonoran desert.

Species name	Abbreviation	Family	Habitat	Habit
<i>Fraxinus velutina</i> Torr.	<i>Fv</i>	Oleaceae	R	WD
<i>Populus fremontii</i> Wats.	<i>Pf</i>	Salicaceae	R	WD
<i>Prosopis velutina</i> Woot.	<i>PvR</i>	Fabaceae	R	WD
<i>Salix gooddingii</i> Ball	<i>Sg</i>	Salicaceae	R	WD
<i>Tamarix ramosissima</i> Ledeb	<i>Tr</i>	Tamaricaceae	R	WD
<i>Baccharis salicifolia</i> (Ruiz & Pav) Pers	<i>Bsl</i>	Compositae	F	WD
<i>Baccharis sarothroides</i> Gray	<i>Bsr</i>	Compositae	F, U	DD/PS
<i>Acacia constricta</i> Benth.	<i>Ac</i>	Fabaceae	U	WD
<i>Acacia greggii</i> Gray	<i>Ag</i>	Fabaceae	U	WD
<i>Cercidium microphyllum</i> (Torr.) Rose & Johnston	<i>Cm</i>	Fabaceae	U	DD/PS
<i>Prosopis velutina</i> Woot.	<i>PvN</i>	Fabaceae	U	WD
<i>Ambrosia dumosa</i> (Gray) Payne	<i>Ad</i>	Compositae	U	DD
<i>Encelia farinosa</i> Gray	<i>Ef</i>	Compositae	U	DD
<i>Fouquieria splendens</i> Engelm.	<i>Fs</i>	Fouquieriaceae	U	DD
<i>Juniperus monosperma</i> (Engelm.) Sarg.	<i>Jm</i>	Cupressaceae	U	E
<i>Larrea tridentata</i> (DC.) Cov.	<i>Lt</i>	Zygophyllaceae	U	E

possibility is that there are disadvantages to having xylem that is overly resistant to cavitation for the prevailing  $\Psi_x$  requirements of a habitat. There may be a trade-off between safety from cavitation during drought and hydraulic efficiency when soil moisture is high (Zimmermann, 1983; Sobrado, 1993; Tyree, Davis, and Cochard, 1994; Alder, Sperry, and Pockman, 1996). This trade-off could arise if increased resistance to cavitation necessitated smaller diameter conduits with lower conducting capacity or if the smaller diameter pit membrane pores associated with increased resistance to cavitation caused a reduction in  $k_x$  (e.g., Schulte and Gibson, 1988). In either case, if the lower hydraulic efficiency of cavitation-resistant plants resulted in slower growth or limited resource acquisition under wet soil conditions that otherwise favored growth, species with less negative  $\Psi_{crit}$  could have a competitive advantage over those with more negative  $\Psi_{crit}$ . While montane trees (Sperry et al., 1994) exhibited no relationship between cavitation vulnerability and hydraulic efficiency, a larger survey (Tyree, Davis, and Cochard, 1994) found a weak correlation between cavitation vulnerability and conduit diameter, a proxy for hydraulic efficiency. Another potential disadvantage of cavitation-resistant xylem may be that it requires more energy and structural material to produce (Wagner, Ewers, and Davis, 1998; Hacke, Sperry, Pockman, and Davis, unpublished data).

It is also possible that safety margins above  $\Psi_{crit}$  are small because there are direct advantages to cavitation under drought conditions. Cavitation may contribute to drought survival by rationing water use to maximize seasonal extraction of soil moisture reserves (Sperry, 1995). Water released by cavitating conduits can rehydrate drought-stressed leaves (Dixon, Grace, and Tyree, 1984; Lo Gullo and Salleo, 1992). Cavitation in easily replaced or short-lived tissues such as roots or leaves (Zimmermann, 1983; Tyree and Ewers, 1991; Tyree et al., 1993; Sperry, 1995) may protect larger, long-lived structures such as stems during extreme drought. Similarly, cavitation in fine root junctions of desert succulents can decouple them from drying soil (Nobel and Cui, 1992; North and Nobel, 1992) limiting water loss via the roots during extended drought.

This paper addresses the relationship between cavitation resistance and species distributions within a small geographic area. Specifically, we predicted that we would observe increas-

ingly negative  $\Psi_{crit}$  in plants at more and more xeric microsites reflecting plant distribution with respect to water availability. This prediction was addressed by surveying cavitation vulnerability across Sonoran desert species adapted to a wide range of water availability—from riparian to desert upland habitats. These habitats represent a moisture gradient from perennially wet soil in the riparian zone to seasonally very dry soil in the uplands. We measured cavitation vulnerability of 15 species and estimated safety margins based on  $\Psi_x$  at the height of the summer drought of 1995. We also compared  $\Psi_x$ , transpiration ( $E$ ), and in situ cavitation before and after the drought to assess how closely each species approached  $\Psi_{crit}$  ( $=\Psi_x$  causing complete loss of  $k_x$ ). Water transport properties and anatomy of stem xylem that relate to hydraulic efficiency were measured to see whether a trade-off with cavitation resistance was present. Finally we re-evaluated previously published data on cavitation, habitat, and conducting efficiency in light of our results from Sonoran desert species.

## MATERIALS AND METHODS

**Research site**—The study was conducted at the Cienega Creek Natural Preserve, Pima County, Arizona (32°01' N, 110°37' W, elevation 1036 m) during the period April–October 1995. The site includes a perennial riparian zone (described by Hendrickson and Minckley, 1984) located in close proximity to desert habitat. We studied 15 species (from eight families) spanning the spectrum of water availability at the site (Table 1). These species included most of the dominant species in the area and several patterns of vegetative phenology. All individuals used in the experiments occurred within 1 km of each other. Five individuals of each species were labeled for measurements of transpiration and  $\Psi_x$ . Individuals adjacent to these plants were sampled for vulnerability curves.

The precipitation and temperature at the site are typical of southeastern Arizona. Mean annual precipitation 11 km from the site averaged 310 mm (SD = 69.6) over a 31-yr period (Sellers and Hill, 1974). Mean monthly precipitation (Fig. 1A) over the same period showed an April–June drought and monsoon rains in July and August. Mean monthly precipitation was highly variable as indicated by its coefficient of variation (Fig. 1A). Long-term mean daily maximum temperatures in Tucson (32 km west) exceed 32°C from May to September (Fig. 1B).

**Xylem pressure ( $\Psi_x$ )**—Leaf xylem pressure was measured in April and early July 1995 using a Scholander pressure chamber (PMS Instrument, Cor-

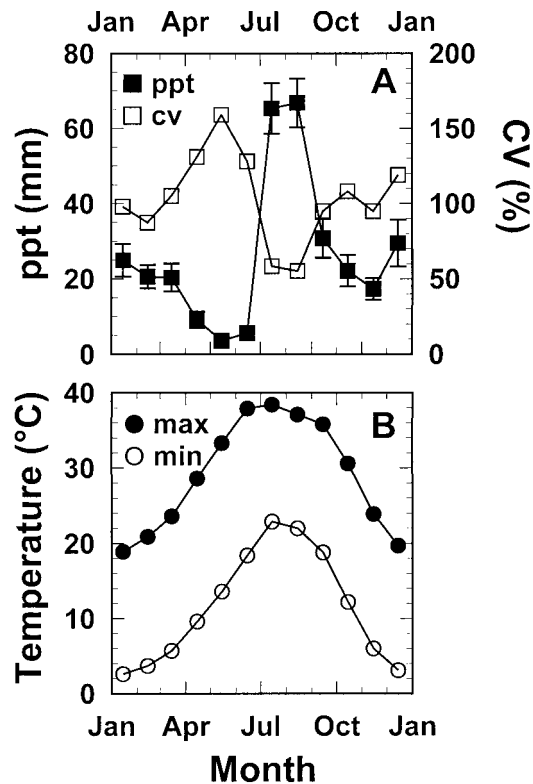


Fig. 1. Long-term climate data for sites near Cienega Creek Natural Preserve, Pima County, Arizona. (A) Mean monthly precipitation at N Lazy H Ranch located 11 km from the site for the period 1942–1972 and the coefficient of variation (CV) of the mean for each month (Sellers and Hill, 1974). (B) Mean maximum and minimum temperatures at the University of Arizona, Tucson, Arizona located 32 km from the study site.

vallis, Oregon, USA). Two shoot tips from each of the five labeled plants were collected and measured at predawn (0400–0530) and at midday (1200–1400). A plastic bag containing a moist paper towel was placed around the shoot before it was cut from the plant with a sharp razor blade or clippers. After the shoot was excised, the bag was immediately sealed to prevent water loss. These bags were placed in a lightproof container to avoid solar heating. Shoots were held in bags until measurement, which occurred within 15 min of collection (Turner, 1987). The pressure chamber was used to measure *C. microphyllum* even when no microphylls were present. Leaf  $\Psi_x$  in *S. gooddingii* was not measured in April 1995, but average data from April 1993 and 1994 are included for comparison (W. T. Pockman and J. S. Sperry, unpublished data). Predawn and midday leaf  $\Psi_x$  in *F. splendens* were estimated using leaf disc psychrometers (J. R. D. Merrill Specialty Equipment, Logan, Utah, USA) because the absence of a petiole in this species makes pressure chamber measurements difficult. Psychrometers were individually calibrated using NaCl solutions. Samples were collected with a leaf punch at the same time as those of other species and immediately sealed in a psychrometer chamber (Oosterhuis and Wullschlegel, 1987). Psychrometers were placed in an insulated container and held 30–90 min for vapor- and thermal-equilibration (Brown and Chambers, 1987) before being measured with a microvoltmeter (model PR-55, Wescor Inc, Logan, Utah, USA).

The minimum stem  $\Psi_x$  of the April and July measurements ( $\Psi_{xmin}$ ) was used to estimate the minimum safety margins ( $\Psi_{xmin} - \Psi_{crit}$ ) for each species. For most species  $\Psi_{xmin}$  was the July measurement. To estimate stem  $\Psi_x$  in April, we measured  $\Psi_x$  of bagged leaves or twigs attached directly to stems of the size used in the vulnerability curve measurements (see below). Flow is minimized through bagged organs, promoting equilibration of  $\Psi_x$  with the subtending stem. To eliminate transpiration, leaves or twigs were wrapped in

aluminum foil the evening before measurement. Bagged organs were excised and measured with the pressure chamber at the same time that midday leaf  $\Psi_x$  was determined. To facilitate measurement of all species in a short period at the height of the drought in July, stem  $\Psi_x$  was estimated as the same fraction of the difference between predawn and midday leaf  $\Psi_x$  observed in the April measurements. This approach assumes that any changes in hydraulic conductance of the flow path from soil to stem were equally distributed along the flow path.

**Transpiration rate**—Transpiration at ambient humidity was measured on 3–5 leaves of each of the five labeled plants of each species at the beginning (April) and end (early July) of the summer drought. Measurements were made using a steady-state porometer (model LI-1600, LICOR, Lincoln, Nebraska, USA) equipped with the cylindrical chamber head (model 1600-07). Absolute transpiration was recorded in the field and later corrected by dividing by the actual area of the measured leaves collected following measurement. Although transpiration measured this way may not accurately reflect in situ transpiration (McDermitt, 1990), we used these data only as a relative measurement.

Transpiring surface area was determined (or estimated for non-laminar structures) using a leaf area meter (LI-COR LI-3100). Areas for species with non-laminar transpiring surfaces were calculated. For twigs of the stem photosynthetic shrubs (*C. microphyllum* and *B. sarothroides*) the total area was calculated as the area of any leaves (or microphylls) plus the surface area of the stem. Stem surface area of *C. microphyllum* was calculated as a conical frustum using caliper measurements of diameter at both ends and the length of the green portion of the twig. Similarly, stem area of square-stemmed *B. sarothroides* was calculated as four times the average width of the green stem multiplied by its length. For *J. monosperma*, the area measured by the leaf area meter was the projected area of a cylinder, and the actual surface area was estimated by multiplying the projected area by  $\pi$ .

**Native embolism measurements**—Native embolism refers to xylem blockage associated with in situ cavitation. We measured it on stem segments of each species using the hydraulic conductivity method of Sperry et al. (1988). In early morning, one branch was collected from each of seven plants in the field and transported to the laboratory inside plastic bags containing a moist paper towel to prevent desiccation. In the laboratory, a stem segment ~100 mm in length and 5 mm in diameter was cut from each branch while it was held underwater to prevent the introduction of additional air emboli. The segment ends were trimmed with a sharp razor blade to eliminate any flow restrictions introduced when stems were cut. Segments were fitted with gaskets and installed in a tubing manifold for measurement of hydraulic conductivity ( $k_h$  = mass flow rate per pressure gradient). Each stem was measured individually by applying gravity-induced pressure of <10 kPa and measuring the flow through the stem. In these and all other hydraulic measurements, we used an HCl solution adjusted to a pH of 2 and filtered to 0.22  $\mu$ m to retard microbial growth in the tubing manifold. Tests in woody tissue show no effect of this solution relative to water on hydraulic parameters (Sperry and Saliendra, 1994). Since this work we have switched to using filtered water as a measuring solution and controlling microbial growth with frequent bleaching of the tubing system. After the initial  $k_h$  measurement ( $k_{hi}$ ), stems were repeatedly flushed with solution at 100 kPa (to remove embolism) until  $k_h$  measured between flushes reached a maximum ( $k_{hd}$ ). Embolism was quantified as the percentage  $k_{hi}$  was below  $k_{hd}$ .

$$\text{percentage embolism} = 100(1 - k_{hi}/k_{hd}). \quad (1)$$

The embolism arising during the drought was determined from the difference in embolism between April and July measurements.

**Vulnerability curves**—Vulnerability curves of all species (except *A. dumosa*) were estimated in stem segments using an air-injection method (Sperry and Saliendra, 1994). According to the air-seeding mechanism (Zimmermann, 1983), the negative  $\Psi_x$  required to pull air into a conduit and cause cavitation is equal and opposite to the positive air pressure required to push air into that conduit when  $\Psi_x$  is equal to atmospheric pressure. This equality has been verified for a number of conifers and angiosperm species (Sperry and Tyree,



1990; Sperry, Perry, and Sullivan, 1991; Cochard, Cruiziat, and Tyree, 1992; Sperry and Saliendra, 1994; Jarbeau, Ewers, and Davis, 1995; Alder, Sperry, and Pockman, 1996; Sperry et al., 1996) including two of the species studied here (*S. gooddingii* and *P. fremontii*; Pockman et al., 1995). This relationship allows vulnerability curves (the decline in  $k_h$  with decreasing  $\Psi_x$ ) to be estimated by measuring the decline in  $k_h$  as increasing air pressure is applied around the xylem.

Branches of each species were collected in the field (one per plant), misted with water, triple bagged in plastic to prevent desiccation, and transported to the laboratory. Stem segments 0.22–0.55 m in length were cut from each branch underwater, side branches removed, and the ends trimmed with a sharp razor blade. Prior to determination of the vulnerability curve, stem segments were flushed with solution at 100 kPa for 20 min. This insured that the vulnerability curve included all potentially functional xylem rather than just the xylem that was functional at the time of collection. Flushed segments were inserted through a double-ended pressure sleeve with both ends protruding. Rubber compression gaskets, held in place by aluminum end caps, formed an airtight seal so the sleeve pressure could be increased around the stem. One end of the stem was attached to tubing allowing the measurement of  $k_h$  by applying a hydraulic head and measuring the flow through the segment. Measurements of  $k_h$  were made gravimetrically by collecting the flow from the stem in tared vials filled with absorbent paper. During all  $k_h$  measurements, sleeve pressure was held at 0.1 MPa to avoid leakage of solution from any exposed xylem inside the sleeve. Since this work was completed we have found that the 0.1 MPa pressure is usually unnecessary, and less variation results if the sleeve pressure is dropped to atmospheric.

Stem  $k_h$  was measured after exposure of the segment to progressively higher air pressure in the sleeve. Elevated pressures were held constant for 10–20 min before being decreased to 0.1 MPa and held for 10 min prior to the  $k_h$  measurement. The  $k_h$  was not measured at the higher sleeve pressure because rapid airflow through embolized xylem interfered with collection of solution from the exposed segment end. After each increase in air pressure, the percentage embolism was calculated (Eq. 1) where  $k_{hi}$  was the current segment  $k_h$  and  $k_{hi}$  was the  $k_h$  prior to exposure to pressure above 0.1 MPa. Depending upon species, air pressure was increased in 0.5-, 1-, or 2-MPa increments until the embolism percentage was >95%. The vulnerability curve was plotted as percentage embolism vs.  $\Psi_x$  where  $\Psi_x$  was predicted as the negative of the applied air pressure. To determine whether these vulnerability curves were consistent with field observations, we compared native embolism at  $\Psi_{xmin}$  with the vulnerability curve for each species.

We used a dehydration method (Sperry, Donnelly, and Tyree, 1988) for measuring vulnerability curves to corroborate the results of the air injection method (*L. tridentata*) or where the air injection method yielded inconsistent results because of resinous secretions (*E. farinosa*). Stems were collected in the field, transported to the laboratory where they were allowed to dehydrate either on the bench-top or, to speed the process, in the sun outside of the laboratory. Stems were then placed in a plastic bag with a moist paper towel for 30 min to allow  $\Psi_x$  to equilibrate throughout the stem before  $\Psi_x$  was measured with a pressure chamber. Percentage embolism was determined on stem segments using the native embolism procedures described above.

Vulnerability curves were used to calculate mean cavitation  $\Psi_x$  and  $\Psi_{crit}$ . To calculate mean cavitation  $\Psi_x$ , vulnerability curves were replotted to show the incremental (rather than cumulative) increase in percentage embolism associated with each decrease in  $\Psi_x$ , or " $\Psi_x$  class." The mean cavitation  $\Psi_x$  for this distribution was determined using the midpoint of each  $\Psi_x$  class. This procedure was performed for the entire vulnerability curve for comparison with measures of xylem conduit diameter and hydraulic efficiency, which were measured on all conduits from a stem cross section (see below). For comparison with  $\Psi_{xmin}$ , mean cavitation pressure was also determined for vulnerability curves that were scaled to begin with the native embolism level observed in the field (see Results). This procedure yields the mean cavitation pressure of the conduits that were functional at the time of collection. The  $\Psi_{crit}$  was estimated as  $\Psi_x$  at 100% embolism using a third-order polynomial fitted to the vulnerability curve data. In some cases this procedure resulted in value of  $\Psi_{crit}$  that was slightly more negative than our pressurization data (e.g., *T. ramosissima*). The  $\Psi_{crit}$  of *A. dumosa* was taken from Mencuccini

and Comstock (1997) for comparison with our measurements of water potential and transpiration in this species.

**Hydraulic efficiency parameters—Conduit diameter**—Conduit diameter is an important determinant of hydraulic efficiency because flow is proportional to the fourth power of the radius of the conduit (Zimmermann, 1983). Conduit diameter distributions were measured on all stems used for vulnerability curves. Transverse sections of stems were cut using a sliding microtome or by hand with a razor blade. The lumens of all xylem conduits within a randomly chosen radial sector were traced using a light microscope with a drawing tube attachment and a digitizing tablet (Donsanto Corp., Micro-Plan II, Natick, Massachusetts, USA). To reflect the diameter distribution of all xylem in the stem (vs. one growth ring), a sector was defined as all xylem within a radial sector defined by ray parenchyma. Additional sectors were measured completely until a minimum of 200 conduits was measured from each stem. The digitizing tablet software calculated the maximum diameter and cross-sectional area of each conduit lumen traced. Diameter distributions were then calculated using 10- $\mu$ m classes based on both the actual percentage of conduits in each class (frequency distribution) and on the estimated percentage of total conductance contributed by each class (hydraulic distribution). The mean of this hydraulically weighted distribution is given by  $\Sigma r^5$  divided  $\Sigma r^4$  where  $r$  is conduit radius. We refer to this as the "hydraulic mean." Hydraulically weighted distributions and means were used because our measurements of native embolism and vulnerability to cavitation were based on hydraulic conductivity.

For comparison with published data, we also calculated the mean diameter of the conduits that account for 95% of the flow ( $D_{95}$ ) through stems of each species (Tyree, Davis, and Cochard, 1994). This was accomplished by sorting the list of measured conduit diameters in descending order, calculating the fourth power of each value and the total  $\Sigma r^4$ . Then, the fourth powers were summed again, from largest to smallest, until the value was 95% of total  $\Sigma r^4$  and the mean diameter of this subset of conduits ( $D_{95}$ ) was calculated.

**Specific conductivity ( $k_s$ )**—A direct measure of hydraulic efficiency is the specific conductivity ( $k_s$ ), defined as the  $k_h$  divided by the conducting area. The  $k_s$  was calculated by dividing the maximum  $k_h$  of each stem (from native embolism measurements) by cross-sectional area of the whole stem. Cross sectional areas were measured using a digitizing tablet.

## RESULTS

**Vulnerability curves and native embolism**—Figures 2–4 show vulnerability curves of all species obtained on flushed stems where embolized xylem was initially refilled. The curves show a rather surprising portion of very vulnerable xylem that should be cavitared for typical  $\Psi_x$  measured in the field. Consistent with this observation was the high native embolism of many of these same species (Table 2), most in excess of 50%. Native embolism showed a 1:1 correspondence with the embolism predicted from vulnerability curves for native  $\Psi_x$  (native embolism =  $0.949(\text{predicted embolism}) + 9.65$ ,  $r = 0.682$ ,  $P < 0.01$ ). Dye perfusions of flushed and native stems indicated that most of the highly vulnerable and thus permanently embolized conduits were in older xylem. Thus, the functional xylem was only a small proportion of the total xylem that was refilled during the flushing process. To represent the vulnerability of the functional xylem to cavitation we based the mean cavitation pressure (Fig. 5B) on "scaled" vulnerability curves (not shown) which showed the percentage loss of conductivity with xylem pressure relative to the native embolism values in July.

**Riparian vs. upland species—Xylem pressure**—Predawn and midday  $\Psi_x$  in riparian vs. upland species (Fig. 5A) reflected the extreme differences in water availability between these

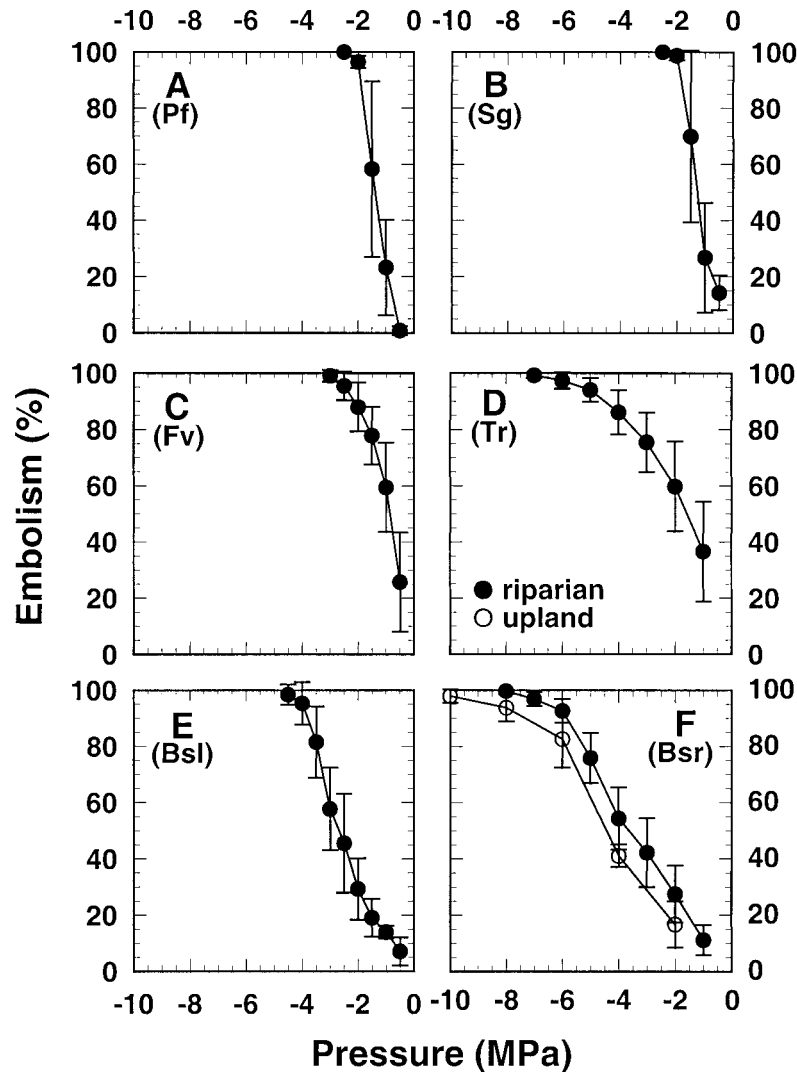


Fig. 2. Estimated  $\Psi_x$  causing cavitation in riparian and floodplain species as measured using the air pressure method. The mean percentage embolism relative to initial hydraulic conductance is shown at each pressure applied (closed circles  $\pm 1$  SD,  $N = 5$  or 6). Vulnerability to cavitation of an upland population of *B. salicifolia* is also shown for comparison (panel F, open circles  $\pm 1$  SD,  $N = 4$ ). Species abbreviations are as in Table 1.

habitats. Predawn  $\Psi_x$  was greater than  $-1.2$  MPa throughout the study in all riparian species except *T. ramosissima*. In contrast, among the upland species, April predawn  $\Psi_x$ 's were between  $-0.7$  and  $-3$  MPa and August values ranged from  $-2$  to less than  $-10$  MPa. The lowest  $\Psi_x$  among desert upland shrubs were 3–6 times lower than the minimum midday  $\Psi_x$  among riparian species. Two upland species, *F. splendens* and *E. farinosa* became deciduous during the summer drought.

**Vulnerability to cavitation,  $\Psi_{crit}$  and safety margins**—Mean cavitation pressure and  $\Psi_{crit}$  are shown in Fig. 5B. The lower  $\Psi_x$  experienced by desert upland species was associated with greater resistance of these species to cavitation compared to riparian species (Figs. 5, 6). The significant correlation ( $r = 0.8521$ ,  $df = 14$ ,  $P < 0.01$ ) between mean cavitation pressure and  $\Psi_{xmin}$  (Fig. 6A) indicated that vulnerability to cavitation reflected water availability.

The  $\Psi_{crit}$  was also correlated with  $\Psi_{xmin}$  (Fig. 6B,  $r = 0.8376$ ,  $df = 13$ ,  $P < 0.01$ ). In all species,  $\Psi_{xmin}$  was above

$\Psi_{crit}$ , indicating positive safety margins from transport failure. Safety margins ranged from 1.0 to 9.4 MPa and showed a tendency to increase with decreasing  $\Psi_{xmin}$  (although the slope in Fig. 6B is not significantly different from 1).

The vulnerable xylem of the obligate riparian species (*F. velutina*, *P. fremontii*, *S. gooddingii*; Fig. 2A–C) would not allow them to transport water over the range of  $\Psi_x$  exhibited by most other species in the study (Fig. 6B). Similarly, the xylem of the most xeric species (*A. dumosa*, *E. farinosa*, *J. monosperma*, and *L. tridentata*; Fig. 4) developed  $\Psi_{xmin}$  that was low enough to completely cavitate all other species, upland as well as riparian (Fig. 6B). Between these extremes, a larger group of riparian (*Baccharis* spp., *T. ramosissima*; Figs. 2D–F) and upland (*Acacia* sp., *C. microphyllum*, *F. splendens*, *P. velutina*; Figs. 3–4) species exhibited intermediate values of mean cavitation pressure and  $\Psi_{crit}$  (Figs. 5B, 6B).

**Hydraulic efficiency and conduit diameter**—Although upland species could easily tolerate the  $\Psi_{xmin}$  observed in the

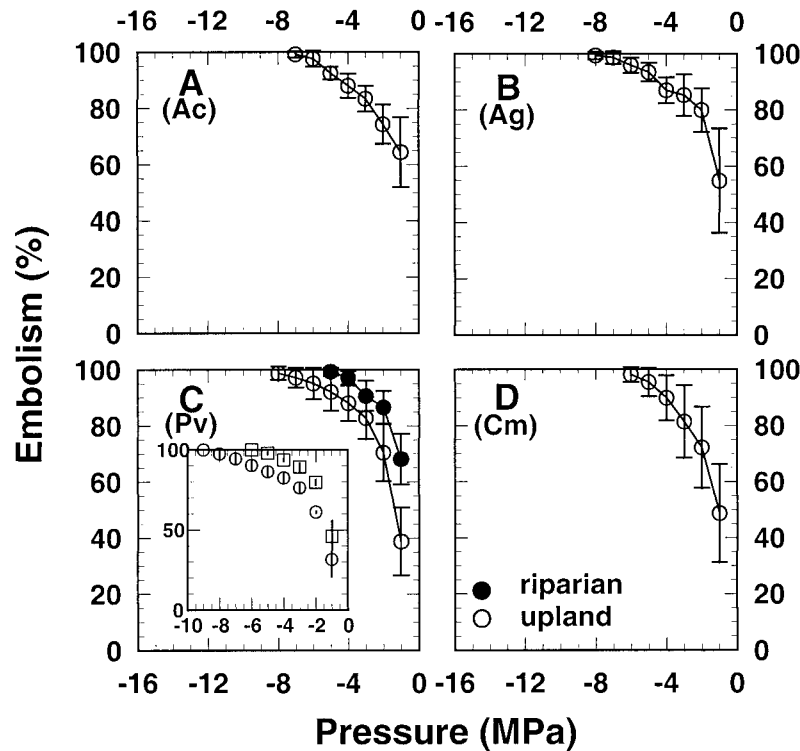


Fig. 3. Estimated  $\Psi_x$  causing cavitation in four upland representatives of the Fabaceae measured using the air pressure method. Percentage embolism relative to initial hydraulic conductance is shown at each pressure applied (open circles  $\pm 1$  SD,  $N = 5$  or 6). The vulnerability curve is also shown for a riparian population of *P. velutina* for comparison (panel C, solid circles  $\pm 1$  SD,  $N = 6$ ). The two vulnerability curves observed for upland individuals of *P. velutina* are shown in the inset of panel C. Species abbreviations are as in Table 1.

riparian area, few of these species occurred there. Was this associated with a trade-off between vulnerability to cavitation and hydraulic efficiency? To answer this question, we compared mean cavitation pressure with hydraulic mean diameter (Table 3) and  $k_s$  (Fig. 5D). Mean cavitation pressure of the nonconiferous species was significantly correlated with mean hydraulic diameter (Fig. 7A;  $r = 0.6214$ ,  $df = 12$ ,  $P < 0.05$ ) and with  $k_s$  (Fig. 7B;  $r = 0.7602$ ,  $df = 12$ ,  $P < 0.01$ ) suggesting a trade-off between cavitation vulnerability and conducting efficiency. Correlations with both the hydraulic mean and  $k_s$  were also significant when *J. monosperma* was included but, not surprisingly, it had a strong effect on the relationship (Fig. 7). These data indicated that across the species studied increased conduit diameter was generally associated with decreased cavitation resistance.

Although only a few species occurred in both riparian and upland habitats, our estimates of  $k_s$  (Fig. 5D) suggested that only the upland species with the highest  $k_s$  were found in riparian sites and that only the riparian species with the lowest  $k_s$  occurred in more xeric sites. *Prosopis velutina*, *A. constricta*, and *A. greggii* were the only upland species observed in riparian sites. The mean  $k_s$  of each of these species was  $>2 \text{ kg} \cdot \text{s}^{-1} \cdot \text{MPa}^{-1} \cdot \text{m}^{-1}$ , significantly different from most other upland species and the same as most riparian species. Upland species with  $k_s$  lower than  $2 \text{ kg} \cdot \text{s}^{-1} \cdot \text{MPa}^{-1} \cdot \text{m}^{-1}$  were strictly desert species that were never observed in or around riparian sites. Of the primarily riparian species, only *B. sarothroides* was occasionally observed at desert upland sites. The  $k_s$  of *B. sarothroides* was 5–10 times lower than most other riparian

species (Fig. 5D). The nonnative riparian *Tamarix ramosissima* was not significantly different in  $k_s$  than the native riparian species despite the fact that it was much more resistant to cavitation.

**Native embolism**—Despite the broad range of  $\Psi_x$  experienced by upland species during the summer drought, little or no increase in native embolism occurred between April and July (Table 2). In a majority of the species sampled, percentage embolism remained constant or decreased between April and July (Table 2). Percentage embolism decreased in *A. constricta*, *T. ramosissima*, and in both *Baccharis* species, suggesting that xylem production occurred between April and July and/or that previously embolized vessels had become irreversibly blocked by tyloses during that time. Refilling of embolized vessels with water may also occurred, but seemed unlikely given that the period was one of progressive drought and decreasing  $\Psi_x$ . Dye perfusions showed no evidence of refilling of previous year's xylem. Small but significant increases in native embolism (Table 2) were detected in *P. fremontii* and *A. dumosa*. Both species approached  $\Psi_{crit}$  relatively closely during drought.

**Transpiration**—In April, the transpiration rate (Fig. 5C) showed no trend across the range of  $\Psi_x$  in riparian and upland habitats (Fig. 5A). However, in July when  $\Psi_x$  of most species was at  $\Psi_{xmin}$ , transpiration decreased linearly across species with declining predawn  $\Psi_x$  until about  $-4 \text{ MPa}$  ( $r = 0.8488$ ,  $df = 10$ ,  $P < 0.01$ ). Below this  $\Psi_x$ , July transpiration was

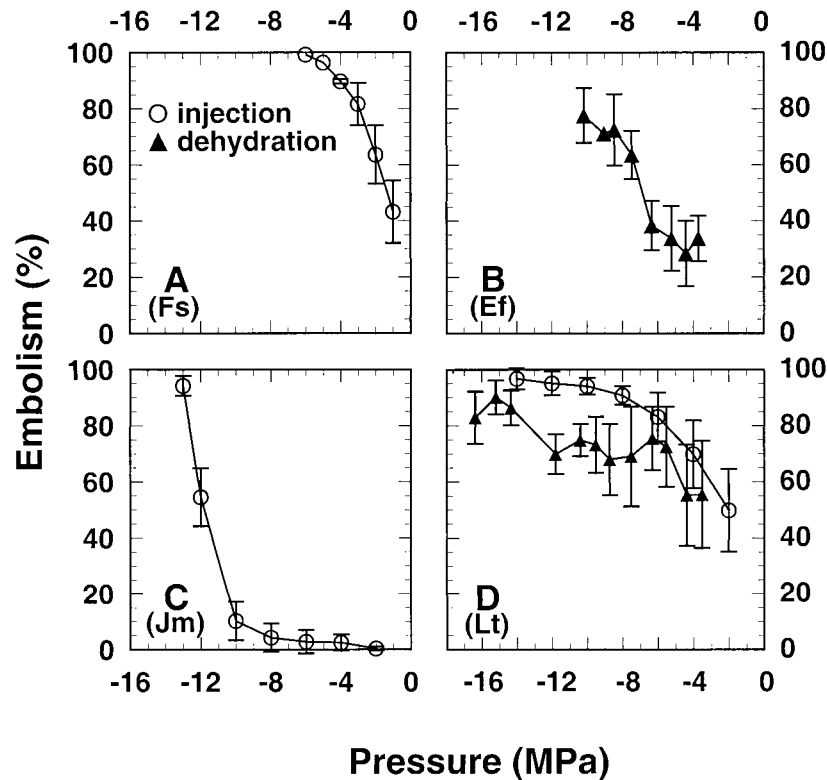


Fig. 4. Estimated  $\Psi_x$  causing cavitation in four desert upland species measured using the air pressure method. The dehydration method was used for comparison in *L. tridentata* and was the sole method used for *E. farinosa* because of anomalous results from the air pressure method (panels B, D; triangles  $\pm$  1 SD). Species abbreviations are as in Table 1.

near zero (Fig. 5C). The riparian species were thus not only the most vulnerable to cavitation and exhibited the smallest safety margins from  $\Psi_{crit}$ , but they also had the highest transpiration rates in July.

**Comparisons within riparian and upland species—Xylem pressure**—Besides the differences in  $\Psi_x$  between riparian and upland species, there was also considerable variation within

TABLE 2. Mean native embolism of stems in April and July of 1995.<sup>a</sup>

Species	April (1995)		July (1995)	
	Embolism (%)	SD	Embolism (%)	SD
Fv	67.70	16.40	60.42	27.01
Pf	16.50	3.20	31.97**	6.40
PvR	74.40	19.50	66.21	13.21
Sg	15.83	15.80	15.39	10.39
Tr	86.90	5.64	46.95**	20.37
Bsl	67.40	15.20	11.37**	7.83
Bsr	48.14	0.49	21.63**	7.74
Ac	95.30	3.65	86.51	6.45
Ag	70.18	11.50	76.20	18.20
Cm	38.82	15.04	26.86	25.63
PvN	89.02	5.77	62.88	12.48
Ad	84.87	5.74	93.35**	7.60
Ef	34.93	10.76	32.72	11.28
Fs	69.64	16.37	72.74	15.33
Jm	10.63	7.49	23.98	15.63
Lt	66.70	10.80	55.70	15.57

<sup>a</sup> July measurements are marked (\*\*) where there were significant differences between April and July. Species abbreviations are as in Table 1.

each group. Obligate riparian trees (*F. velutina*, *P. fremontii*, and *S. gooddingii*) exhibited high predawn  $\Psi_x$  (Fig. 5A), which decreased only slightly between April and July, as did midday  $\Psi_x$  (Fig. 5A). Predawn  $\Psi_x$  in *F. velutina* was significantly lower than in nearby individuals of *P. fremontii* (Fig. 5A; Student's *t* test,  $t = 7.1759$ ,  $df = 8$ ,  $P < 0.01$ ). The mean predawn  $\Psi_x$  in both *Baccharis* species was lower than nearby riparian trees and decreased between April and July. Predawn  $\Psi_x$  was unexpectedly low in *T. ramosissima* (Fig. 5A) considering that all individuals were within 5 m of a perennial stream. Perhaps our predawn measurements of this species were influenced by significant nocturnal transpiration or growth induced water uptake.

An even greater range of  $\Psi_x$  was observed among the upland species. Although predawn  $\Psi_x$  in several upland species was greater than  $-1$  MPa in April, the decrease in  $\Psi_x$  between April and July ranged from 0.5 MPa in *C. microphyllum* to over 9 MPa in *A. dumosa*. Many of the species at the extremes of this range occurred adjacent to each other (e.g., *F. splendens*, *A. dumosa*, and *L. tridentata*) suggesting that the variation in  $\Psi_x$  was related to differences in rooting depth.

**Vulnerability to cavitation and safety margins**—The same correlations observed across species between mean cavitation pressure and  $\Psi_{crit}$  vs.  $\Psi_{xmin}$  were also significant when species groups from riparian and upland communities were considered alone. Among riparian species, the native trees (*F. velutina*, *P. fremontii*, and *S. gooddingii*) were the most vulnerable to cavitation (Fig. 2A, B, C) with a  $\Psi_{crit}$  of  $-2$  to  $-3$  MPa; *F.*



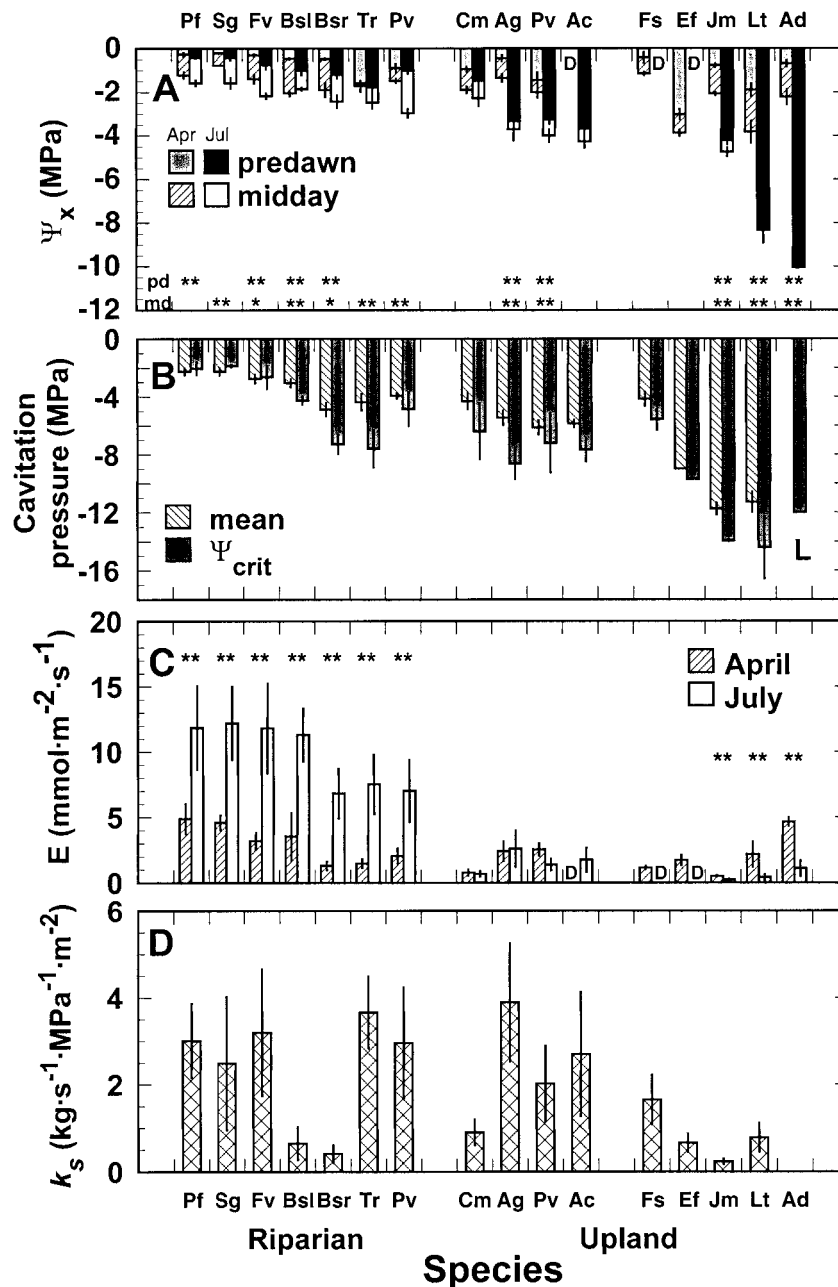


Fig. 5. Summary of stem xylem pressure, cavitation pressure, transpiration and specific conductance for 15 species in the Sonoran desert. (A) Stem xylem pressure ( $\Psi_x$ ) measured at predawn (light and dark shaded bars) and midday (hatched and open bars) in April and July 1995. The letter D indicates species that were deciduous at the time of measurement. At the bottom of the panel, significant differences between April and July  $\Psi_x$  are indicated by asterisks in each species' column for predawn (top row) and midday (bottom row) measurements. (B) Mean cavitation pressure of each species calculated for scaled vulnerability curves (hatched bars  $\pm 1$  SD,  $N = 5$ ) and  $\Psi_{crit}$  for each species (shaded bars). The critical pressure for *Ambrosia dumosa* (Ad), marked with an "L", is taken from Mencuccini and Comstock (1997). (C) Mean transpiration rate ( $E$ ,  $\pm 1$  SD,  $N = 5$ ) measured at midday in April and July 1995. Significant differences between April and July measurements are marked (Student's  $t$  test,  $df = 8$ ,  $*P < 0.05$ ,  $**P < 0.01$ ). (D) The mean specific conductivity ( $k_s$ ,  $\pm 1$  SD,  $N = 5$ ) of flushed stem segments of each species. Species abbreviations are as in Table 1.

*velutina* was slightly more resistant than the other two species in accordance with its lower  $\Psi_{xmin}$ . Interestingly, the nonnative *T. ramosissima* (Fig. 2D) had a  $\Psi_{crit}$  of  $-7$  to  $-8$  MPa, 3–4 times more resistant to cavitation than the surrounding native riparian trees. It also had the second largest safety margin in the riparian community (1.9 MPa, smaller only than *B. sarothroides*). Of the two *Baccharis* species, *B. salicifolia* (Fig.

2E), restricted to the floodplain, was more vulnerable to cavitation than *B. sarothroides* (Fig. 2F), whose range extended to disturbed sites in the desert upland. The vulnerability curves of floodplain and upland populations of *B. sarothroides* were similar except for a lower  $\Psi_{crit}$  in the upland population (Fig. 2F).

The upland individuals of the four species of Fabaceae all



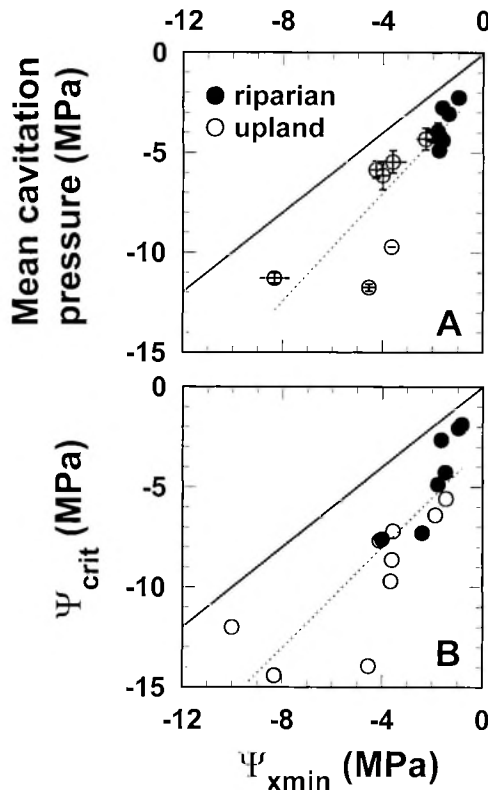


Fig. 6. Mean cavitation pressure and the critical xylem pressure ( $\Psi_x$ ) compared to minimum  $\Psi_x$  ( $\Psi_{xmin}$ ) measured in the same species during this study. (A) Mean cavitation pressure of riparian (open symbols) and upland (solid symbols) species for scaled vulnerability curves. A linear regression through all data was significant ( $r = 0.9146$ ,  $N = 14$ ,  $P < 0.01$ ). (B) The pressure required to induce 100% embolism ( $\Psi_{crit}$ ) was calculated using a third order polynomial fitted to the vulnerability curve data for each stem. Each point is the mean of all stems for each species ( $\pm 1$  SD,  $N = 5$ ). The  $\Psi_{crit}$  was significantly correlated with  $\Psi_{xmin}$  ( $r = 0.8989$ ,  $N = 15$ ,  $P < 0.01$ ).

TABLE 3. Mean actual and hydraulic diameter, maximum diameter, total number of conduits ( $n$ ), and number of individuals ( $N$ ) measured for each species studied.

Species	Actual diameter ( $\mu\text{m}$ )		Hydraulic diameter ( $\mu\text{m}$ )		Maximum diameter ( $\mu\text{m}$ )	$n$	$N$
	Mean	SD	Mean	SD			
<i>Fv</i>	29.15	5.03	76.82	14.96	150	1301	6
<i>Pf</i>	26.89	1.79	44.54	2.94	80	1179	5
<i>PvR</i>	33.00	6.38	86.66	7.99	150	1248	6
<i>Sg</i>	28.24	4.99	44.98	3.61	90	1076	5
<i>Tr</i>	31.60	7.01	58.30	6.64	100	1285	6
<i>Bsl</i>	22.74	3.34	39.38	5.64	80	1346	6
<i>Bsr</i>	19.03	1.82	28.68	3.40	70	1983	8
<i>Ac</i>	37.67	4.89	82.76	12.69	180	2107	9
<i>Ag</i>	36.96	3.48	86.44	15.09	170	1328	6
<i>Cm</i>	33.32	4.06	62.42	5.90	130	1305	6
<i>PvN</i>	34.19	5.60	70.55	5.03	120	1303	6
<i>Ef</i>	24.86	2.84	40.43	6.23	110	1113	5
<i>Fs</i>	26.84	2.20	36.32	2.05	85	1390	6
<i>Jm</i>	8.65	0.76	10.46	0.86	25	859	4
<i>Lt</i>	22.16	2.26	30.70	2.69	70	1421	6

had a  $\Psi_{crit}$  of  $-6$  to  $-8$  MPa (Fig. 3). *Prosopis velutina* (Fig. 3C) sampled in the riparian area within metres of surface water was more vulnerable ( $\Psi_{crit} = -5$  MPa) than some similar size individuals in the surrounding desert uplands ( $\Psi_{crit} = -7$  to  $-8$  MPa). Three of the six individuals sampled at the upland site had vulnerability curves that were not different from those measured in the riparian area, while the other three were significantly more resistant to cavitation (Fig. 3C, inset).

The other desert upland species exhibited a broad range of vulnerability curves. The drought-deciduous *Fouquieria splendens* (Fig. 4A) had a  $\Psi_{crit}$  of  $-6$  MPa, which was more vulnerable to cavitation than both *T. ramosissima* and *B. sarothroides* in the floodplain. The two evergreen plant species in the desert upland were the most resistant to cavitation of all the species studied. *Juniperus monosperma* (Fig. 4C) did not begin to cavitate until pressures below  $-10$  MPa and had a  $\Psi_{crit}$  of  $-13$  MPa. Though the endpoint of the *L. tridentata* vulnerability curve was ambiguous (see below), extrapolation

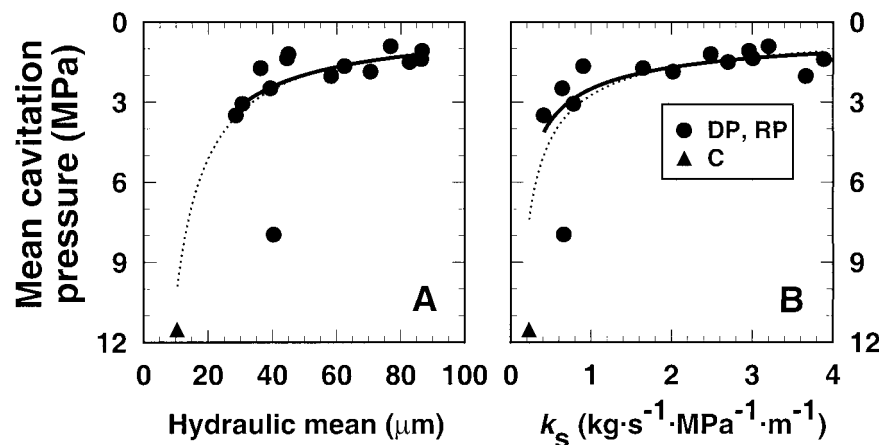


Fig. 7. (A) The mean cavitation pressures of each species as a function of mean hydraulically weighted diameter. Symbols denote ring- and diffuse-porous (circles) and coniferous (triangles) wood types. Power functions through data for ring- and diffuse-porous species (solid line,  $r = 0.6214$ ,  $df = 12$ ,  $P < 0.05$ ) and all species (broken line,  $r = 0.6404$ ,  $df = 13$ ,  $P < 0.05$ ) were significant. (B) The mean cavitation pressures of each species as a function of mean specific conductivity ( $k_s$ ). Symbols are as in panel A. Power functions for ring- and diffuse-porous species (solid line,  $r = 0.7602$ ,  $df = 12$ ,  $P < 0.01$ ) and all species (broken line,  $r = 0.8612$ ,  $df = 13$ ,  $P < 0.01$ ). Mean cavitation pressure for both panels was calculated using unscaled vulnerability curves because flow and anatomical data represent all xylem in each stem (see Materials and Methods).

suggested a  $\Psi_{crit}$  of  $-14$  MPa or lower (Fig. 4D). *Ambrosia dumosa* growing at Organ Pipe Cactus National Monument, Arizona, has been shown to have an  $\Psi_{crit}$  of approximately  $-12$  MPa (Mencuccini and Comstock, 1997).

**Conduit diameter and hydraulic efficiency**—Among the desert upland species, the four representatives of the Fabaceae, together with *T. ramoissima* and *F. velutina* in the riparian area, exhibited the largest mean diameter and hydraulic mean diameters of the species studied (Table 3). Despite their large conduits, these species were considerably less vulnerable to cavitation than most of the riparian species discussed previously (Figs. 2, 3). Both actual and hydraulic diameter distributions exhibited a smaller range among the desert shrub species. The mean diameters were quite similar among *F. splendens*, *E. farinosa*, and *L. tridentata* (Table 3) even though their  $\Psi_{crit}$  ranged from  $-6$  MPa to at least  $-14$  MPa (Fig. 4).

## DISCUSSION

The comparison between  $\Psi_{xmin}$  and  $\Psi_{crit}$  (Fig. 6B) indicated that most riparian species would be completely cavitared at the  $\Psi_x$  that occurred in the xeric upland habitat. Given that cavitation resistance is to some extent genetically determined (Kavanagh, Bond, and Knowe, 1999; Kolb and Sperry, 1999a), the implication is that it has an important influence on the distribution of plants with respect to water availability. Consistent with this is the observation that seedling mortality has been correlated with extensive cavitation (Williams, Davis, and Portwood, 1997). Cavitation-induced mortality in seedlings and in mature individuals during extreme drought may thus combine to exert an important influence on species distribution.

The relationship that we observed between  $\Psi_{crit}$  and  $\Psi_{xmin}$  within a narrow geographic area was reinforced when we combined our data with available values from the literature (Fig. 8A). These data, from plants native to a broad array of mesic and arid, tropical and temperate habitats on three continents, indicated that the plants in this study (Fig. 8A, solid circles) spanned the entire range of  $\Psi_x$  for which vulnerability curves have been measured. The persistence of the relationship across the combined data suggests that vulnerability to cavitation is of general relevance to plant distribution across habitats.

Based on our data and the literature survey, xeric species tend to have a larger safety margin from  $\Psi_{crit}$  than mesic species (Figs. 6, 8). There are several factors concerning both  $\Psi_{xmin}$  and  $\Psi_{crit}$  that contribute to this trend. Seasonal studies of *S. gooddingii*, *P. velutina*, and *L. tridentata* at the same site suggest that the size of the safety margin is related to the predictability of water availability (Pockman and Sperry, unpublished data). The small safety margins of the obligate riparian species are associated with an abundant perennial water supply and therefore a consistent  $\Psi_{xmin}$  from year to year. These plants can survive with a small safety margin because they experience predictable water stress. At the other extreme, the evergreen species (*J. monosperma*, *L. tridentata*) experience wide variation in water availability and  $\Psi_{xmin}$  through the seasons. They require large safety margins as insurance against periodically severe drought. Xeric species will also tend to have large safety margins because the  $\Psi_{xmin}$  measured during a short-term study is likely a significant underestimate of the  $\Psi_{xmin}$  experienced over the plant lifetime. Many of the study species can live 50–100 yr or longer (Goldberg and Turner,

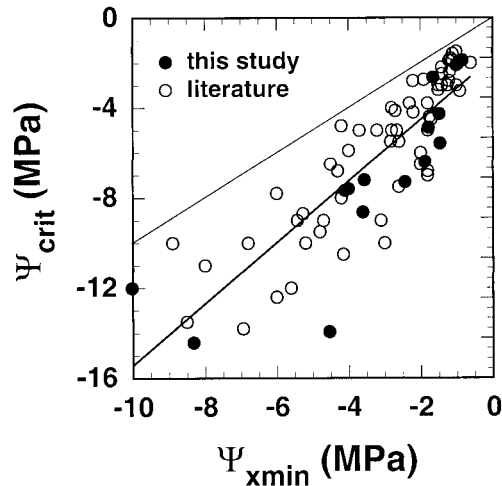


Fig. 8. The limits to water stress ( $\Psi_{crit}$ ) vs. minimum xylem pressure ( $\Psi_{xmin}$ ) in all species from this study (solid circles) and all available species from the literature representing a range of habitats and lifeforms (open circles).  $\Psi_{crit}$  was significantly correlated with  $\Psi_{xmin}$  ( $r = 0.85$ ,  $df = 70$ ,  $P < 0.01$ ). This relationship did not change substantially when data were replotted using genus or family averages. Data are from this study and published values (Sperry, Tyree, and Donnelly, 1988; Tyree and Sperry, 1988, 1989; Cochard and Tyree, 1990; Sperry and Tyree, 1990; Cochard, 1992; Cochard, Cruziat and Tyree, 1992; Newfield et al., 1992; Sperry and Sullivan, 1992; Lo Gullo and Salleo, 1993; Tyree et al., 1993; Cochard, Ewers, and Tyree, 1994; Kolb and Davis, 1994; Machado and Tyree, 1994; Sperry et al., 1994; Sperry and Saliendra, 1994; Tyree et al., 1994; Zotz, Tyree, and Cochard, 1994; Jarbeau, Ewers, and Davis, 1995; Alder, Sperry, and Pockman, 1996; Redtfeldt and Davis, 1996; Davis, Kolb, and Barton, 1997; Mencuccini and Comstock, 1997; S. D. Davis, unpublished data).

1986; Turner, 1990). The unpredictable climate (Fig. 1A) of the region means that there will be occasional droughts much more severe than we observed. Longer term monitoring of  $\Psi_x$  would tend to reduce safety margins in upland species considerably.

Large safety margins for the upland species in our study may also result from overly negative estimates of  $\Psi_{crit}$ . Our  $\Psi_{crit}$  was based on stem xylem. However, as previously mentioned, under xeric conditions hydraulic failure may occur in the soil before it does in the plant (Sperry et al., 1998) meaning that the actual  $\Psi_{crit}$  would be less negative than predicted from plant xylem. Even if failure did occur in the plant, several studies indicate that it often occurs in root xylem rather than stem xylem under drought conditions (Alder, Sperry, and Pockman, 1996; Mencuccini and Comstock, 1997; Linton, Sperry, and Williams, 1998; Kolb and Sperry, 1999b). This is because the root xylem in woody plants is frequently more vulnerable to cavitation than shoots of the same individuals (Alder, Sperry, and Pockman, 1996; Hacke and Sauter, 1996; Sperry and Ikeda, 1997; Linton, Sperry, and Williams, 1998; Kavanagh, Bond, and Knowe, 1999). In this way, hydraulic failure may be confined to expendable (replaceable) roots rather than the stem, consistent with the “vulnerability segmentation” concept (Zimmermann, 1983; Tyree and Ewers, 1991). The underestimation of  $\Psi_{crit}$  may help explain why, among the least vulnerable upland species, transpiration decreased to near zero while still maintaining large safety margins from the  $\Psi_{crit}$  based on stem xylem (Figs. 5, 6).

While the  $\Psi_{crit}$  data indicate that many of the species in the study could not survive in some of the drier sites (Fig. 6), the

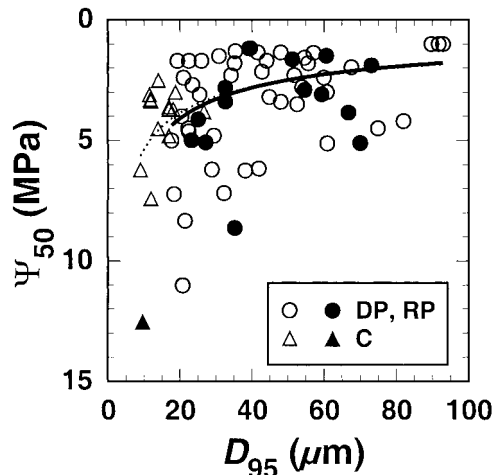


Fig. 9. The  $\Psi_x$  required to induce 50% embolism ( $\Psi_{50}$ ) as a function of the mean diameter of the conduits calculated to account for 95% of the total flow through a stem ( $D_{95}$ ). Solid symbols are species measured in this study. Open symbols are data compiled in Tyree et al. (1994). Data are further divided into coniferous (squares) and diffuse- and ring-porous (circles) wood types. The solid line is a power function through all data for diffuse- and ring-porous wood types ( $r=0.4056$ ,  $df=56$ ,  $P<0.01$ ) and the broken line is a power function including all data ( $r=0.4714$ ,  $df=71$ ,  $P<0.01$ ). These relationships did not change substantially when data were replotted using genus or family averages.

explanation for why cavitation-resistant species are excluded from riparian habitats remains an open question. The assumption is that traits conferring drought tolerance, which would include cavitation resistance, are also traits that compromise growth under favorable conditions. The relationship between vulnerability to cavitation and both measures of hydraulic efficiency (Fig. 7) suggested that resistance to cavitation was achieved at the expense of conducting efficiency. When we plotted  $\Psi_{50}$  against  $D_{95}$  (Fig. 9) for our data combined with published data (Tyree, Davis, and Cochard, 1994) for temperate and tropical trees, shrubs, and vines, we observed a significant correlation between these parameters. This relationship was also significant when the data were averaged by genus or family to compensate for any effects of overrepresentation of phylogenetically related species. While there was no significant relationship among the conifers,  $\Psi_{50}$  was correlated with  $D_{95}$  when all species were considered together. The addition of our data does not substantially change the relationship between  $\Psi_{50}$  and  $D_{95}$  (Fig. 9) reported by Tyree et al. (1994). This relationship accounts for 16% of the variation in the data but is too weak to have much predictive value when comparing specific species pairs (e.g., *E. farinosa* vs. *S. gooddingii*).

The relationship between  $k_s$  and vulnerability to cavitation (Fig. 7) suggests that low  $k_s$  may exclude upland species from riparian habitats where wet soil conditions allow high growth rates. Most species in this study occupied either riparian or desert upland sites but not both. The exceptions were *P. velutina*, both *Acacia* species, and *B. sarothroides*. The high  $k_s$  values of *P. velutina* and *Acacia* spp. (Fig. 5D) may mean that in riparian sites they have the water transport capacity to support the large canopy and substantial transpiration rates that allow them to compete with the obligate riparian species. On the other hand, *B. sarothroides* may escape competition with

high  $k_s$  riparian species because it inhabits the driest of riparian sites and persists through periodic floods that remove most other species.

Increased cavitation resistance has also been linked to increased wood density in one recent study (Wagner, Ewers, and Davis, 1998). Such a relationship might be expected if denser wood is required to sustain the compressive forces generated by lower negative pressures, and to minimize air permeability that might nucleate cavitation. Preliminary data from our study species shows strong support for this relationship (Hacke, Sperry, Pockman, and Davis, unpublished data) and suggests that there is an added construction cost to cavitation resistant xylem. Construction of denser wood may also correspond to slower growth rates (Enquist et al., 1999), further decreasing competitive ability of cavitation resistant species when water is readily available. The picture is thus emerging of several related traits associated with cavitation resistance that together may exclude them from mesic habitats.

The differences in vulnerability between *T. ramosissima* and native riparian vegetation (Fig. 2) may contribute to its ongoing replacement of *S. gooddingii* and *P. fremontii* in riparian areas throughout the American west (Brotherson and Winkel, 1986; Howe and Knopf, 1991). The dominant native riparian trees use groundwater to sustain their large canopies and high transpiration rates (Busch, Ingraham, and Smith, 1992). Along with their profligate water use, such species (Fig. 2; Sperry and Saliendra, 1994; Tyree et al., 1994; Alder, Sperry, and Pockman, 1996) were the most vulnerable to cavitation. Although *T. ramosissima* also maintained high transpiration rates (Fig. 5C), greater resistance to cavitation (Fig. 2) and lower turgor loss points (Busch and Smith, 1995) should confer an advantage when its reliable water supply is interrupted or reduced. Interestingly, despite having xylem more resistant to cavitation than the other riparian species, *T. ramosissima* exhibited similarly high  $k_s$  (Fig. 5D; Smith et al., 1996). Cavitation resistance combined with high  $k_s$  may provide a competitive advantage by allowing it to better tolerate a drop in water table caused by human activity (Smith, Wellington, and Nachlinger, 1991; Stromberg et al., 1992) and by its own transpiration (Vitousek, 1990).

The relationship we observed between  $\Psi_{crit}$  and  $\Psi_{xmin}$  (Fig. 6B) reflects not only the distribution of species with respect to water availability but also the association of cavitation vulnerability with plant traits that influence  $\Psi_{xmin}$ , such as rooting distribution and vegetative phenology. The large differences in  $\Psi_{crit}$  among species growing next to one another emphasize the importance of this association. For example, *F. splendens* and *P. velutina* co-occur with *L. tridentata* despite having substantially higher  $\Psi_{crit}$  (Fig. 5B). Although *F. splendens* is arguably more shallowly rooted than *L. tridentata* (Cannon, 1911), the absence of cavitation in the more vulnerable *F. splendens* (Table 2) suggests that by becoming deciduous it avoids reaching the same  $\Psi_{xmin}$  as *L. tridentata* (Fig. 5A). Although the extent of stem water storage in *F. splendens* has not been determined, this may also play a role in avoiding cavitation or refilling cavitated conduits in this species. The mechanism for this may be similar to shallow-rooted succulents (Nobel and Cui, 1992; North, Ewers, and Nobel, 1992) where cavitation in roots interrupts hydraulic contact with the soil during drought. Although the vulnerability curve of *P. velutina* was similar to *F. splendens* (Figs. 3C, 4A), the deep roots of *P. velutina* (Stromberg et al., 1992) mitigate the ef-



fects of dry shallow soil allowing the species to remain active without cavitation during drought (Table 2).

The small but significant intraspecific differences that we observed between vulnerability curves of *P. velutina* and *B. sarothroides* from different locations within the study site suggest that either vulnerability to cavitation is somewhat plastic in each species or there are distinctly different cavitation genotypes maintained within the population. Previous studies have found a variety of patterns. *Acer grandidentatum* from different microsites exhibited different root vulnerability curves while stems showed no differences (Alder, Sperry, and Pockman, 1996). Other studies have shown genetic differences in vulnerability to cavitation among dispersed populations of the same species (Kavanagh, Bond, and Knowe, 1999; Kolb and Sperry, 1999a) and little divergence when plants of a common origin were transplanted to different microenvironments (Jackson, Irvine, and Grace, 1995). Further study will be required to determine whether the differences that we observed are a result of differential success of distinct genotypes in riparian and upland sites or whether these represent evidence of plastic responses of stem xylem.

Our results show that cavitation could play an important role in determining plant distribution within and between broad habitat types. The combined effects of seedling mortality (Williams, Davis, and Portwood, 1997) and attrition of individuals that become established between climatic extremes may result in the patterns that we observed. Although long-term studies that include physiological data are rare, such efforts and continued study of cavitation during establishment will provide the basis for a mechanistic understanding of the factors that contribute to distribution. A better understanding of the genetic and environmental influence on vulnerability to cavitation is essential if we are to understand the mechanisms resulting in habitat preferences. The role of cavitation and hydraulic efficiency in determining rates of water extraction and growth may also provide useful insight into the mechanisms of competitive exclusion (Eissenstat and Caldwell, 1988) of drought-adapted species in mesic habitats. Vulnerability to cavitation represents an important adaptation to growth under various water regimes, and it may also prove useful for understanding vegetation change in response to local, regional, and global changes in environmental conditions.

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